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THE MORPHOLOGY OF THE SEED OF BUCKWHEAT

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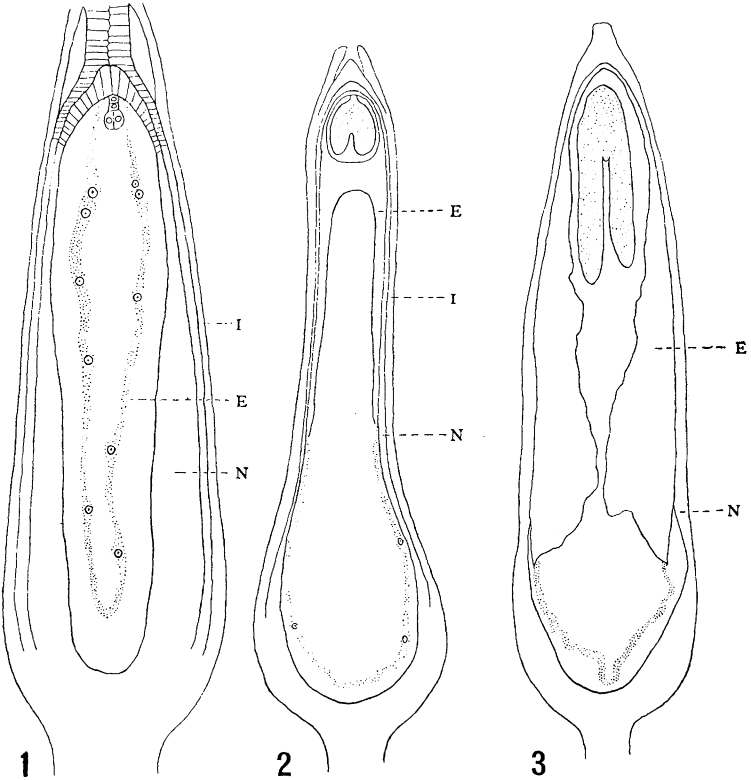
(WITH EIGHT FIGURES)

The Polygonaceae have been several times referred to in recent literature as being characterized by the production of seeds having an abundant perisperm (JOHNSON **7**, p. 337; COULTER and CHAMBERLAIN **3**, p. 179). This character has been taken by JOHNSON as an indication of rather close relationship between the Polygonaceae and the Piperaceae, in which family he has observed a perisperm. These statements as to the seed of the Polygonaceae are apparently based on the work of HARZ (**4**, p. 1072), who includes this family among the "Curvembryonaten," which he characterizes as "Eine grosse natürliche Gruppe . . . . alle ausgezeichnet durch den Besitz eines reichlichen mehlhaltigen Perisperms und eines meist peripherisch gelagerten Embryo." HARZ (p. 1102) figures and describes in considerable detail the structure of the buckwheat seed, and evidently considers the entire storage region as perisperm. He also states that the same condition occurs in species of *Rumex*. KRAEMER (**9**), to be sure, speaks of the Polygonaceae as having an endosperm, but does not discuss the morphology of the seed.

A careful study of the seed of *Fagopyrum esculentum* has convinced the writer that in this genus at least no perisperm is present at maturity. The material used in this study was collected during the summer of 1910 and fixed in Juel's fluid (JUEL **8**). Microtome sections were used exclusively. These were cut rather thick, usually about 12μ, and stained with Delafield's haematoxylin.

The early development of the embryo appears to be typical in every respect. In fact, up to the stage at which the cotyledons begin to be differentiated, the embryo corresponds almost cell for cell with the often figured *Capsella Bursa-pastoris*, in which, however, the suspensor is considerably longer.

Free nuclear division apparently begins in the embryo sac soon after fertilization, and by the time the embryo has reached the quadrant stage (fig. 1), the endosperm contains at least 32 nuclei, held in the thin peripheral layer of cytoplasm. The nucellus at this stage is principally in the lower half of the ovulary cavity. A single layer, however, differing markedly from the rest, extends to the micropyle. This outer layer becomes differentiated some time before fertilization, and consists of closely packed, regular cells, characterized by the possession of rather dense granular contents and the absence of a vacuole.



FIGS. 1–3.—Fig. 1, longitudinal median section of ovule, showing the embryo in the quadrant stage and the endosperm in the free nuclear condition; the cells of the outer layer of the nucellus and the inner layer of the integument are outlined in the micropylar region; ×100; fig. 2, similar section about the time the cotyledons are first differentiated in the embryo; the upper portion of the endosperm has become cellular, while no cell walls have appeared in the lower portion; ×33; fig. 3, later stage, showing further development of the embryo and of the cellular portion of the endosperm; ×25; *I*, integuments; *N*, nucellus; *E*, endosperm.

Growth and nuclear division are most rapid in the upper portion of the endosperm, that is, in the region between the growing embryo and the degenerating nucellar tissue. Cell formation begins in this region about the time the cotyledons first appear in the embryo. The cells arise centripetally and with great regularity. Apparently only a single nucleus is included in each cell, and there is no evidence of nuclear fusions. Cell formation gradually extends both above and below the region where it originates, and soon a marked differentiation is evident in the endosperm. At the stage shown in fig. 2, cell formation has progressed till a portion of the endosperm, some 8 or 10 cells thick, extends entirely across, just below the embryo. Above, around the developing embryo, the endosperm consists of only a single layer of cells; while below the thickest region, the endosperm becomes thinner, consisting toward the bottom of fewer and fewer layers of cells; till at the base, for at least a third of its length, the endosperm does not become divided into cells at all, but consists merely of a layer of cytoplasm with scattered nuclei, enclosing a large sap cavity.

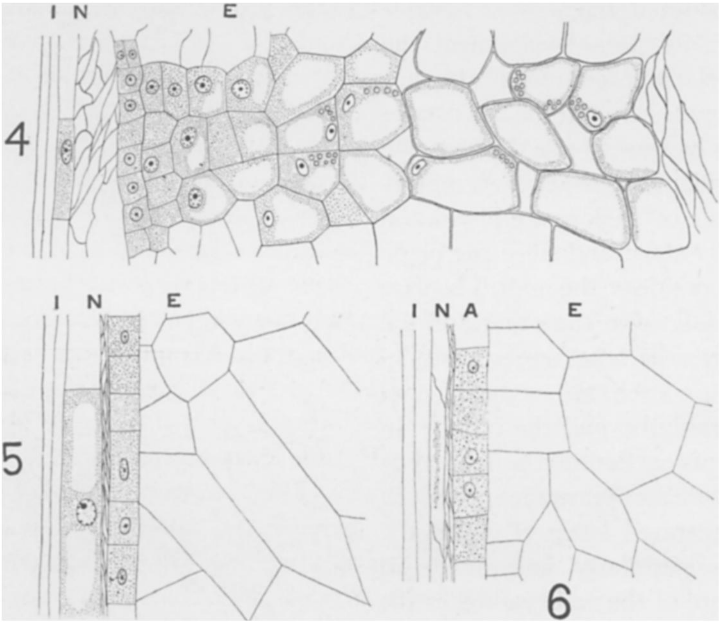
This marked differentiation of the endosperm into two regions, one of which shows no cell formation whatever, suggested the chambered embryo sacs described by HOFMEISTER (**5**, p. 185), STRASBURGER (**11**, p. 111), and others, in which the first division of the primary endosperm nucleus is followed by the formation of a cross wall, dividing the embryo sac into two chambers, in only one of which the endosperm is developed. Careful study of early stages makes it seem certain, however, that no such cross wall occurs in the embryo sac of the buckwheat.

Soon after the stage just described, a secondary differentiation becomes evident in the cellular portion of the endosperm; the outer layer taking on the appearance and function of a cambium layer, which cuts off cells only on the inner side. A similar condition has been figured by CHAMBERLAIN (**2**, p. 344) in the developing endosperm of *Dioon edule*. These "cambium" cells divide rapidly; and the continued growth of the cells thus formed forces the wall of the ovary outward, and causes the more central portion of the endosperm to extend downward toward the base of the ovule. No further development occurs in the lower portion of the original embryo sac (fig. 3). At the same time, the embryo is developing at the expense of the inner portion of the endosperm, so that the cells of the endosperm at this stage differ considerably in appearance. The "cambium" cells and the cells adjacent to them are thin-walled and closely packed. Nearer the center the cells become larger and vacuolate, some of them containing a considerable amount of starch; their walls also become slightly thicker, and the continued growth of the ovule pulls them apart, so that intercellular spaces of considerable size occur. Of the cells nearest the embryo only the crushed and distorted walls remain (fig. 4, *E*).

Nearly all the nucellar tissue has been destroyed by this time. The differentiated outer layer, however, persists in an actively growing condition, differing from the earlier stages only in that the cells have elongated and show, in some instances, small vacuoles (fig. 4, *N*). This outer layer of the nucellus is apparently composed of two quite different regions, which grade insensibly into each other. The upper portion, around the micropyle, consists of a plate of cells which apparently undergo no change after the time of fertilization. The cells of the lower portion continue to grow actively with very little if any cell division. They increase somewhat in thickness, and to a very marked degree in surface extent, keeping pace with the growth of the young seed. As the embryo nears maturity, these cells become more and more coarsely vacuolate (fig. 5, *N*), and in the mature seed only the crushed remains of this layer are present (fig. 6, *N*).

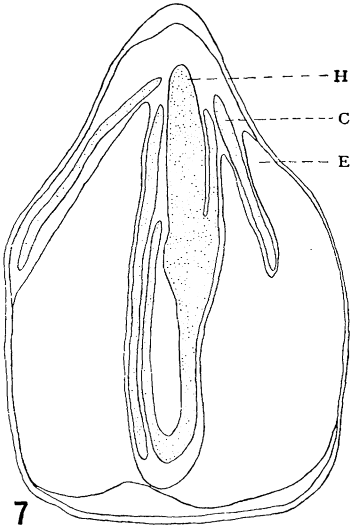
The fact that this layer persists in an actively growing condition till the growth of the endosperm is practically complete, together with the dense granular nature of the cell contents, suggests that it has a nutritive function, the "nutritive jacket" of COULTER and CHAMBERLAIN (**3**, p. 103). Similar layers, presumably nutritive in function, have been observed in numerous instances. Usually this "nutritive jacket" is derived from the integument; in one case however, *Armeria plantaginea*, BILLINGS (**1**, p. 278) describes such a layer, which he calls a "tapetum," as derived from the outer portion of the nucellus. In *Erodium gruinosum* BILLINGS finds this "tapetum" two layers thick, one layer of cells being derived from the integument and one from the nucellus. He describes a "tapetum" derived from the integument in numerous genera, notably *Linum*, *Geranium*, *Primula*, *Phacelia*, and *Lobelia*.

LLOYD (**10**, p. 103) has recently shown that in the date the integument serves to some extent to distribute nutritive material to the developing endosperm. In the buckwheat, however, the integuments seem to have no part in this process. In fact, they undergo very little differentiation, but remain throughout the growth of the seed as thin, rather uniform structures, each consisting of but two layers of cells. As there are no vessels present in the ovule which might accomplish this work, it seems entirely probable that the outer layer of the nucellus functions for the transfer of nutritive



FIGS. 4–6.—Fig. 4, portion of longitudinal section at about the stage shown in fig. 3; only the outer layer of the nucellus, the "nutritive jacket," remains functional; the endosperm shows an outer layer of embryonic cells and a more central region of large vacuolate cells; some of the larger cells contain starch grains; ×260; fig. 5, later stage; the cells of the nutritive jacket have become vacuolate; ×260; fig. 6, mature grain; the nucellus remains merely as a thin region of crushed cells; the outer layer of endosperm cells is differentiated as an aleuron layer, the other endosperm cells are crowded with starch; ×260; *I*, integuments; *N*, nucellus; *E*, endosperm; *A*, aleuron layer.

substances from the chalazal region to the growing endosperm. Such an explanation might account for the fact that the endosperm develops fastest in the upper portion, the broken down cells of the nucellus forming, lower down, an effective barrier to the passage of food material.



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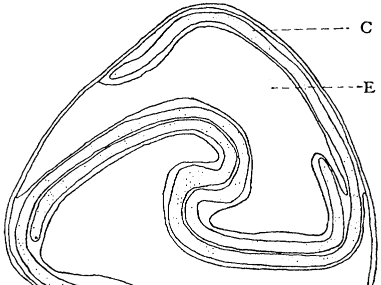

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FIGS. 7, 8.—Fig. 7, longitudinal median section of mature seed; ×15; fig. 8, transverse section of mature seed, below the hypocotyl; ×15; the parts of the embryo are shaded; *E*, endosperm; *C*, cotyledons; *H*, hypocotyl.

In its later development the embryo becomes remarkably unsymmetrical, and as the cotyledons increase in size they become considerably curved. At maturity the cotyledons are broad and rather thin; and since the blade on one side of the midrib is twice as wide as on the other and the midribs lie together, one cotyledon on each side extends considerably beyond the other. In a cross section of the seed they present the appearance of a much exaggerated letter S (fig. 8, *C*). This peculiarly unsymmetrical nature of the embryo makes the endosperm exceedingly irregular.

Shortly before the seed is mature, a further differentiation takes place in the endosperm. The cambium layer, after it has ceased cutting off starch storing cells, divides further by anticlinal walls; thus forming a continuous layer of short regular cells, filled in the mature seed with dense granular contents, but containing no starch. This is an aleuron layer, the "eiweisshaltige Zellen" of HARZ (fig. 6, *A*). Except for this single aleuron layer, the irregular endosperm consists of large, closely packed cells, filled with starch. In its development the cellular portion has been crowded well down toward the base of the ovule. Even in the mature fruit, however, a space containing the remains of the undeveloped basal portion of the embryo sac is always present in the chalazal region (fig. 7).

The absence of a perisperm in the buckwheat does not of course exclude the possibility of its occurrence in other members of the Polygonaceae. That such a variation is sometimes found in nearly related genera is shown by the work of HUMPHREY (**6**) on the Scitaminales. In this order HUMPHREY found a progressive series of stages in the development of the endosperm. The Musaceae have a large starch bearing endosperm, in the Zingiberaceae and Cannaceae the endosperm is thin and contains only aleuron, while in the Marantaceae it is apparently not present in the mature seed. Variation occurs, as HUMPHREY shows, even within a single family. Among the Musaceae, *Heliconia* shows a distinct, though rather thin, starch bearing perisperm, while in *Strelitzia* only a thin layer of nucellar tissue showing no cellular structure remains in the mature seed. It is interesting to note that in the latter genus the massive endosperm never wholly fills the cavity of the seed, a condition comparable to that noted by the writer in *Fagopyrum*.

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LITERATURE CITED

1. BILLINGS, FREDERICK H., Beiträge zur Kenntnis der Samenentwickelung. Flora **88**:253–318. 1901.
2. CHAMBERLAIN, C. J., The ovule and female gametophyte of *Dioon*. BOT. GAZ. **42**:321–358. 1906.
3. COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of angiosperms. New York. 1903.
4. HARZ, C. O., Landwirthschaftliche Samenkunde. Berlin. 1885.
5. HOFMEISTER, W., Neuere Beobachtungen über Embryobildung der Phanerogamen. Jahrb. Wiss. Bot. **1**:82–188. 1858.
6. HUMPHREY, JAMES E., The development of the seed in the Scitamineae. Ann. Botany **10**:1–37. .1896.
7. JOHNSON, D. S., On the development of certain Piperaceae. BOT. GAZ. **34**:321–338. 1902.
8. JUEL, H. O., Die Tetradenteilungen bei *Taraxacum* und anderen Cichoriaceen. Kgl. Svenska Vet. Akad. **39**^{4}:1–20. 1905.

9. KRAEMER, HENRY, A text-book of botany and pharmacognosy. Ed. 4. Philadelphia. 1910.
10. LLOYD, F. E., Development and nutrition of the embryo, seed, and carpel in the date, *Phoenix Dactylifera* L. From the 21st Ann. Rep. Missouri Bot. Garden. 103–164. 1910.
11. STRASBURGER, E., Zellbildung und Zelltheilung. Ed. 3. Jena. 1880.